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Research Article

Niche partitioning of invasive Amur sleeper (*Perccottus glenii*) amongst native fish communities in three different freshwater ecosystems

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Abstract

The invasive fish, Amur sleeper, poses a significant and growing threat to Central European freshwater ecosystems. Despite its rapid spread, the ecological implications of its invasion have been poorly explored. Recent findings confirm its presence in various Estonian freshwater systems, raising concerns about its imminent expansion into larger lakes. To better understand its potential ecological impacts, we explored the isotopic niche of the Amur sleeper in comparison with native fish species co-existing in three Estonian freshwater ecosystems. We employed carbon and nitrogen stable isotope analyses alongside gut content analyses. Our findings show that the Amur sleeper's diet in newly-invaded Estonian water bodies predominantly comprises benthic macroinvertebrates, although it may also include fish, confirming its role as a predator in the local food web. Notably, Amur sleeper populations exhibited clear isotopic niche partitioning in three invaded ecosystems. A logistic regression model, based on stomach content analyses, revealed an ontogenetic diet shift from benthivorous to piscivorous feeding habits from small to large specimens. Amur sleeper exhibits voracious, non-selective feeding habits, which can negatively impact native freshwater communities. The ability to occupy a distinct isotopic niche, with minimal overlap with native fish populations, may reduce interspecific competition, facilitating the spread and establishment of Amur sleeper in newly-invaded habitats. Managing the spread of this invasive species thus becomes even more critical to safeguard the integrity of native aquatic ecosystems.

Key words: gut content, invasive species, isotopic niche, native fish community, ontogenetic shift, stable isotopes

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Introduction

The spread of invasive alien species is recognised as one of the greatest threats to global biodiversity (Roy et al. 2024). Freshwater ecosystems are particularly vulnerable to biological invasions where invasive species can lead to significant ecological effects, altering community structures and ecosystem processes (Dudgeon et al. 2006; Gallardo et al. 2016). Invasive freshwater fish species can cause strong food web disruption (Wainright et al. 2021), affecting native communities across different

trophic levels (Cucherousset and Olden 2011) and exerting critical top-down and bottom-up effects on the food webs of invaded ecosystems (Britton 2023). Amur sleeper (*Perccottus glenii* Dybowski, 1877) is an invasive fish species that has spread from its natural habitat, the River Amur watershed in far eastern Asia (Reshetnikov 2004, 2013; Covaciu-Marcov et al. 2017; Rau et al. 2017) and has invaded many freshwater ecosystems in central and eastern Europe (Nehring and Steinhof 2015; Rechulicz et al. 2015; Reshetnikov and Karyagina 2015; Kutsokon 2017; Nastase et al. 2019; Kutsokon et al. 2021; Pihlström et al. 2022; Djikanović et al. 2023).

Amur sleeper invasion could alter trophic relationships in aquatic communities by generalist feeding on different trophic levels and prey items mainly associated with submerged vegetation (Grabowska et al. 2009). The wide diet spectrum of Amur sleeper and opportunistic predation with a flexible feeding strategy favours its expansion at the expense of native fauna (Grabowska et al. 2009). Amur sleeper can impact ecosystems via competition with and predation on native species (Grabowska et al. 2009; Kati et al. 2015) and by altering habitats (Reshetnikov 2001, 2003; Plyusnina 2008). The recent, rapid expansion of Amur sleeper into central and eastern European waterbodies will threaten the overall health and biodiversity of local aquatic ecosystems (Grabowska et al. 2009; Somogyi et al. 2023). Studies on the diet of wild Amur sleeper populations in Europe have been conducted by analysing gut contents (Koščo et al. 2008), providing a snapshot of its feeding habits and additional studies were conducted in experimental laboratory conditions (Grabowska et al. 2009; Kati et al. 2015; Grabowska et al. 2019). However, more research is needed to better understand the ecosystem effects of invasive Amur sleeper in natural conditions, its potential impacts on native fish communities and how to improve the efficiency of management actions.

Amur sleeper has already been reported in Estonian freshwater ecosystems (Reshetnikov 2010) and invasion of large Estonian lakes, such as Peipsi and Võrtsjärv, is likely. In 2005, a few specimens of Amur sleeper were captured in the outflowing water channel of the Baltic Thermal Power Plant (BPP), while an abundant (approximately 1 individual per m^2) population was found in a pond close to the Narva Reservoir (Tambets and Järvekülg 2005; Tambets et al. 2010). A few individuals were also found at another site in the Narva Reservoir close to the pond. Amur sleeper was likely introduced by fishermen into the pond and later, during floodings (the pond becomes connected to the reservoir only during high water levels), some individuals escaped and populated the nearby Narva Reservoir.

In summer 2008, northern pike (*Esox lucius* Linnaeus, 1758) were introduced in the pond to eradicate Amur sleeper. Intensive capture and predation by pike and perch reduced the population biomass of Amur sleeper by 80% (Tambets et al. 2010). Although Amur sleeper biomass decreased sharply, the species remained at a low abundance in the pond during the following years.

Due to its feeding habits, ability to exploit a wide spectrum of food resources and rapid invasion rate, it is crucial to better understand the potential ecological effects of the Amur sleeper on native communities for impact assessment and risk management. In this study, we aimed to: (1) evaluate the diet plasticity of invasive Amur sleeper, (2) assess if the species displays a similar isotopic niche in each of the three different invaded ecosystems and (3) quantify its potential overlap with native fish species. We hypothesised that: 1). Amur sleeper has a wider isotopic niche than benthic native fish and 2). Amur sleeper is a strong competitor for local predatory-benthivorous fish species (e.g. perch) due to niche overlap and a similar diet.

Methods

Sampling area

Samples were collected from the Narva Reservoir (59°21.02'N, 28°10.79'E), the cooling water channel of the Baltic Thermal Power Plant (BPP) (59°18.94'N, 28°5.12'E) and a small pond located near, but not connected, to the reservoir (59°21.19'N, 28°11.17'E) (Fig. 1). Narva reservoir is a large (191 km^2) and shallow (average depth 1.8 m) artificial water body located on the Narva River on the border between Estonia and Russia. The reservoir is connected to numerous flowing and stagnant water bodies in the large catchment area of the Narva River (drainage basin 55,800 km^2). The reservoir has an extensive favourable habitat for phytophilous and, in some areas, warm-water fish. The photic zone extends to the bottom in large areas, favouring the growth of vegetation. The BPP channel is connected to the reservoir and water in the sampled part of the channel is warmer than in the reservoir depending on BPP operations. The BPP channel is approximately 15 km long, with mean and maximum depth of 1.8 m and 2.5 m, respectively. Surface area of sampled pond is 0.045 km^2, Secchi depth is 4.5 m and mean and maximum depths are 2.8 m and 7 m, respectively. The bottom of the pond is covered by macrophytes. When we sampled the pond, the oxygen concentration above the macrophyte layer was 8.8 mg/l, while in early spring, this water layer was hypoxic (below 1 mg/l).

Sampling of fish and potential food sources

Samples of Amur sleeper and native fish species were collected in September 2017 from the reservoir, pond and channel using electrofishing and gillnets. Nordic-type, multi-section benthic and pelagic gillnets (5–55 mm from knot to knot) were supplemented with larger mesh sized nets (65 mm from knot to knot). Gillnets were set up overnight in each sampling site and retrieved approximately 15 hours later the next day. Electrofishing (mean area 618 m^2) was performed in shallow water

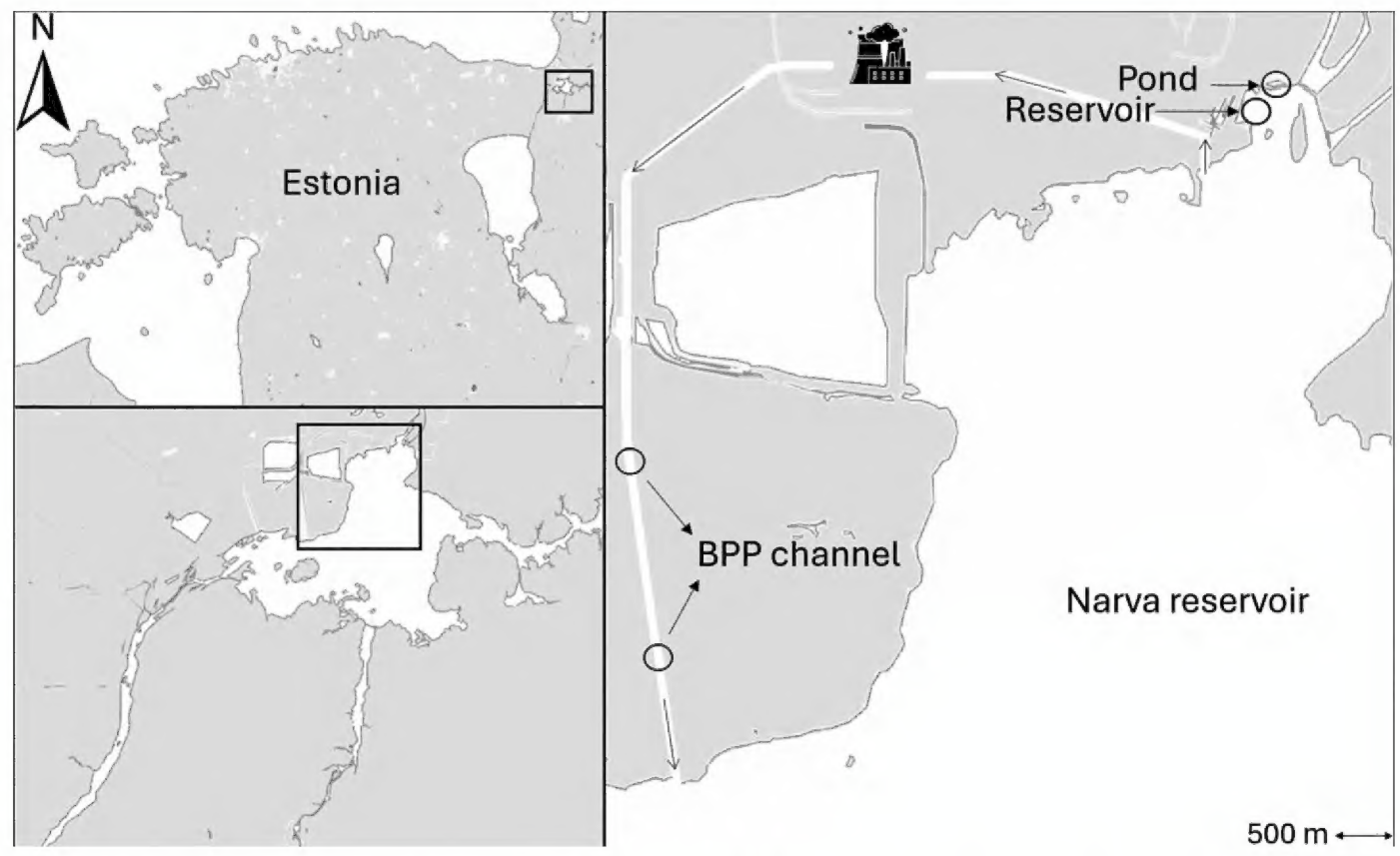

Figure 1. Sampling sites for Amur sleeper, native fish species and macroinvertebrates, as indicated by hollow black circles. Black arrows within the BPP channel indicate the flow direction.

with abundant vegetation near the areas where gillnets were deployed, at the same time or after their removal. The pond was also sampled prior to 2017 and in 2018, using only electrofishing. In September 2017, three replicate samples for macroinvertebrates were collected using a kick-net with a mesh size of 0.5 mm (0.5 to 1.5 m water depth), along littoral areas at sites near where gillnets were set and removed and electrofishing was performed. Additionally, Ekman grab was used to sample macroinvertebrates from the bottom of the pond.

Stable isotope analyses

After sampling, fish and macroinvertebrates were identified to species and at the lowest taxonomic levels, respectively. For stable isotopes analysis (SIA), a piece of white dorsal muscle was collected from each specimen, while macroinvertebrate samples were prepared from whole organisms to represent macroinvertebrate food sources for Amur sleeper (Table 1).

Table 1. Number (n) of macroinvertebrates species sampled in pond, Narva Reservoir and channel and their respective mean values (± standard deviation) of carbon and nitrogen stable isotopes.

Ecosystem	Species	n	$d^{13}C‰$	$d^{15}N‰$
Pond	**Gastropoda**			
	Bithynia tentaculata	3	-29.58 ± 0.66	3.82 ± 0.46
	Crustacea			
	Asellus aquaticus	5	-25.26 ± 0.63	3.35 ± 0.34
	Ephemeroptera			
	Ephemerellidae	5	-26.92 ± 0.79	2.2 ± 0.27
	Coleoptera			
	Dytiscidae	6	-25.55 ± 2.86	4.81 ± 0.65
	Bivalvia			
	Sphaerium sp	9	-32.22 ± 0.31	3.98 ± 0.36
Narva Reservoir	**Gastropoda**			
	Radix balthica	4	-27.67 ± 1.00	8.95 ± 0.44
	Crustacea			
	Asellus aquaticus	6	-26.70 ± 0.27	7.73 ± 1.43
	Gmelinoides fasciatus	16	-25.88 ± 0.75	8.43 ± 1.17
	Bivalvia			
	Dreissena polymorpha	4	-30.75 ± 0.23	10.16 ± 0.08
	Odonata			
	Coenagrionidae	3	-29.25 ± 0.12	11.13 ± 0.07
	Trichoptera			
	Phryganeidae	3	-25.40 ± 3.04	10.69 ± 0.47
BPP channel	**Gastropoda**			
	Lymnaea stagnalis	3	-21.99 ± 0.71	8.18 ± 0.16
	Crustacea			
	Procambarus virginalis	6	-29.09 ± 1.29	8.28 ± 0.62
	Ephemeroptera			
	Caenis horaria	2	-31.02 ± 1.01	6.94 ± 0.12
	Bivalvia			
	Dreissena polymorpha	3	-27.70 ± 0.73	9.3 ± 0.31
	Odonata			
	Aeshnidae	3	-26.66 ± 0.12	9.57 ± 0.02
	Trichoptera			
	Phriganeidae	3	-28.38 ± 0.66	8.84 ± 0.19

All SIA samples were freeze-dried for 48 hours to constant weight, ground to a fine, homogenous powder, weighed into tin cups (~ 0.6 mg of material) and encapsulated. If needed, small macroinvertebrates of the same taxa were pooled to achieve enough material for SIA. Analyses of stable carbon and nitrogen isotopes were conducted using a Thermo Finnigan $DELTA_{plus}$ Advantage continuous-flow isotope ratio mass spectrometer coupled to a Flash EA 1112 elemental analyser (Thermo Scientific, Bremen, Germany) at Jyväskylä University (Finland). SI values for carbon and nitrogen are expressed as parts per thousand (‰) delta values ($\delta^{13}C$, $\delta^{15}N$) relative to international standards:

$$X = (Rsample / Rstandard - 1) \times 1000$$

where X is either carbon or nitrogen SI value and R is the ratio of heavy to light SI of carbon or nitrogen in samples and standards.

Reference materials were used as internal standards, with known relationships to the international standards of The Vienna Pee Dee Belemnite (VPDB) for carbon SI and atmospheric nitrogen (Air-N_2) for nitrogen SI. White muscle tissue of northern pike (*Esox lucius*) and birch leaves (*Betula pendula* L.), with known isotopic compositions, were used as internal working standards to ensure analytical precision. One internal standard was run repeatedly after every five samples in each sequence. Standard deviations within reference samples in each analytical run were always less than 0.1‰ for carbon and 0.2‰ for nitrogen in pike and birch leaf samples. Sample analysis also yielded percentage carbon and nitrogen from which C:N ratios (by weight) were derived.

Isotopic niches

Stable isotope values were used for identifying isotopic niches and to evaluate and compare isotopic niche similarity of Amur sleeper and native fish species in each of the studied freshwater ecosystems. Isotopic niches and isotopic niches overlapping calculations were performed using the *SIBER* (Stable Isotope Bayesian Ellipses in R) package in R (R Core Team 2022). Corrected standard ellipse areas (SEAc) were calculated from the variance and covariance of $\delta^{13}C$ and $\delta^{15}N$ values, corrected for small sample size, as a measurement of the population niche ellipse area for each fish species (Jackson et al. 2011). Each SEAc was calculated by drawing the core of the isotopic niches (40%) to avoid overestimation due to extreme carbon and nitrogen values of individuals. Isotopic niche overlapping was also calculated to assess the degree of ecological similarity between Amur sleeper and native fish species. The overlap was calculated as the proportion of the sum of the non-overlapping areas between two ellipses and expressed as a percentage, ranging from 0, when the ellipses exhibit no overlap, to 1, when the ellipses overlap completely (Jackson et al. 2019).

Stomach content analysis

Amur sleeper is a predatory, omnivorous fish and its diet was assessed by stomach content analyses to support SIA interpretations. Stomach contents were identified and divided into the following categories: macrophytes, zooplankton, macroinvertebrate parts, gastropods, bivalves, Chironomidae, Trichoptera, Ephemeroptera,

Asellus aquaticus, Coleoptera, Odonata, fish, Oligochaeta, Gammaridae, Micronecta and detritus. Stomach fullness was estimated, ranging from 0% (empty stomach) to 100% (full stomach), based on the sum of percentages of each food category (Jensen et al. 2012). The percentage of occurrence (%O_i) of food items in Amur sleeper was calculated as:

$$\%O_i = \frac{J_i}{P} \times 100\%$$

where J_i is the number of Amur sleeper individuals containing prey i and P is the number of Amur sleeper individuals with food in their stomach (Amundsen et al. 1996).

Statistical analyses

To assess the probability of Amur sleeper undergoing an ontogeny diet shift, a logistic regression model was used to estimate the length when individuals could switch their diet from benthivorous to piscivorous feeding habits

$$y = [e^{(\alpha+\beta x)}]\ [1 + e^{(\alpha+\beta x)}]^{-1}$$

where y indicates the occurrence of fish in Amur sleeper stomach, x is the length of Amur sleeper specimens and α and β are the coefficients estimated by the model.

From stomach content analyses, individuals with fish in their stomachs were given the value of 1, whereas those without fish in their stomach were given the value of 0. The logistic regression model was performed in R (R Core Team 2022) using Generalised Linear Model (GLM) with binomial family, library *rms* (Regression Model Strategies), with piscivory as the response variable and length as the predictor variable. Residual analyses were conducted for checking deviation from the distribution, residual dependency on predictor and heteroscedasticity, to validate the Generalised Linear Model (GLM). The regression line was plotted (with 95% of confidence interval) between prey fish occurrence in Amur sleeper stomachs (0 or 1) and the length of analysed Amur sleeper specimens. The feeding behaviour shift to piscivory was set at the individual length where the probability of fish occurrence in the stomachs exceeded 50%. According to the individual total length (TL) set by the logistic regression model, all Amur sleeper specimens were divided in small (TL < 8.7 cm) and large (TL > 8.7 cm) groups. Differences in carbon and nitrogen stable isotopes between small and large Amur sleeper individuals, in each studied ecosystem, were tested using the Mann-Whitney U test. Assumptions for normality and homogeneity of variances were tested prior statistical analyses using Shapiro-Wilk and Levene tests. Variables were transformed if assumptions were not met. All statistical analyses were performed in R (R Core Team 2022).

Results

A total of 66 Amur sleeper individuals were caught: 17 from the pond (4 large and 13 small), 36 from the Narva Reservoir (8 large and 28 small) and 13 from the BPP channel (1 large and 12 small) (Table 2). Amongst the three populations, the smallest individuals appeared in the BPP channel (mean length = 4.50 ± 2.0 cm) compared to the reservoir (7.01 ± 3.27 cm) and pond (7.55 ± 4.45 cm; Table 2). All Amur sleeper individuals collected in the three ecosystems were caught by

Table 2. Number of Amur sleeper and other fish species individuals used for stable isotope analyses and mean values of their length (cm) and carbon and nitrogen stable isotope values (± standard deviation). SEAc indicates the Standard Ellipse Area corrected of each fish population isotopic niche in the pond, Narva Reservoir, and BPP channel. SEAc of Amur sleeper is calculated including large and small specimens. SEAc overlapping % represents the degree of isotopic niche similarity between Amur sleeper and other fish species in each ecosystem.

Ecosystem	Fish species	n	Length (cm)	$d^{13}C‰$	$d^{15}N‰$	$SEAc‰^2$	SEAc overlapping%
Pond	Amur sleeper (*Perccottus glenii*) large	4	14 ± 5.2	-38.19 ± 0.59	9.58 ± 1.82	77.5	–
	Amur sleeper (*Perccottus glenii*) small	13	5.6 ± 1.0	-38.16 ± 10.61	6.79 ± 2.48	–	–
	Roach (*Rutilus rutilus*)	10	20.0 ± 5.1	-38.17 ± 0.95	7.88 ± 0.23	0.43	0
	Rudd (*Scardinius erythrophthalmus*)	5	10.9 ± 2.8	-26.47 ± 1.12	8.10 ± 0.10	0.49	0
	Perch (*Perca fluviatilis*)	9	15.9 ± 2.9	-26.06 ± 1.12	8.80 ± 0.37	1.51	0
	Pike (*Esox lucius*)	4	17.2 ± 3.0	-26.33 ± 0.14	8.08 ± 0.46	0.27	0
Narva Reservoir	Amur sleeper (*Perccottus glenii*) large	8	11.5 ± 2.8	-27.04 ± 0.28	12.86 ± 0.27	0.88	–
	Amur sleeper (*Perccottus glenii*) small	28	5.7 ± 2.0	-27.13 ± 0.52	11.83 ± 0.38	–	–
	Roach (*Rutilus rutilus*)	11	20.8 ± 2.0	-26.46 ± 1.68	13.27 ± 0.75	4.81	14
	Rudd (*Scardinius erythrophthalmus*)	8	22.1 ± 2.6	-24.10 ± 1.86	11.69 ± 1.53	10.7	0
	Perch (*Perca fluviatilis*)	12	23.4 ± 3.4	-26.62 ± 0.66	14.89 ± 0.67	1.53	0
	Ruffe (*Gymnocephalus cernua*)	8	6.8 ± 2.5	-30.02 ± 2.36	11.78 ± 1.45	5.19	0
	Tench (*Tinca tinca*)	4	31.3 ± 8.7	-27.19 ± 0.81	12.87 ± 0.62	2.09	35
	Bleak (*Alburnus alburnus*)	5	11.3 ± 0.8	-29.31 ± 1.28	12.61 ± 0.50	1.66	0
	Spined loach (*Cobitis taenia*)	5	9.4 ± 0.3	-27.78 ± 0.42	12.37 ± 0.28	0.50	32
	White bream (*Blicca bjoerkna*)	6	12.6 ± 1.6	-26.08 ± 0.64	14.01 ± 0.57	1.71	0
BPP channel	Amur sleeper (*Perccottus glenii*) large	1	9.2	-27.64	11.35	0.59	–
	Amur sleeper (*Perccottus glenii*) small	12	4.1 ± 1.6	-29.0 ± 0.45	10.52 ± 0.48	–	–
	Roach (*Rutilus rutilus*)	5	12.1 ± 1.4	-27.04 ± 1.13	12.65 ± 0.91	4.95	0
	Rudd (*Scardinius erythrophthalmus*)	5	23.1 ± 3.7	-23.61 ± 1.33	11.74 ± 0.84	5.93	0
	Perch (*Perca fluviatilis*)	6	19.3 ± 3.5	-26.46 ± 1.39	13.28 ± 0.17	0.93	0
	Spined loach (*Cobitis taenia*)	5	7.4 ± 1.1	-28.74 ± 0.71	12.24 ± 0.54	1.46	0

electrofishing, CPUE was highest in the channel, followed by the reservoir and pond (Table 3). Perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), rudd (*Scardinius erythrophthalmus*) and white bream (*Blicca bjoerkna*) had highest CPUE amongst the fish species collected with gillnets (Table 3).

Isotopic niche widths and overlap of Amur sleeper and native fish communities

SIA results show that values of nitrogen stable isotope of Amur sleeper individuals differ between the pond and reservoir and between the pond and channel, being highest in the reservoir and lowest in the pond (Fig. 2). However, the nitrogen isotope mean values of large Amur sleeper individuals were slightly higher than those of small specimens in the pond (p-value = 0.07) and in the reservoir (p-value < 0.001), while carbon isotope mean values were similar in the pond (p-value = 0.99) and reservoir (p-values = 0.53) (Fig. 2). However, in the pond, small Amur sleeper specimens showed substantial variation of carbon isotope values, with some individuals displaying exceptionally low numbers (Figs 2, 3). Carbon and nitrogen isotopic differences between large and small Amur sleeper individuals in the channel were not tested since, according to the logistic regression model, only

Table 3. Catch Per Unit Effort (CPUE) indicates the number of fish per 100 m^2 of sampling area in electrofishing and the number of fish per net in gillnet sampling, caught in pond, Narva Reservoir and BPP channel.

Place and sampling type	Amur sleeper	Perch	Pike	Roach	Gibel carp	Rudd	Ruffe	Spined loach	Bleak	Tench	White bream
Pond											
Electrofishing	0.2	0	0.3	0	0	0	0	0	0	0	0
Benthic Nordic	–	18.3	0.33	4.3	0	3	0	0	0	0	0
Pelagic Nordic	–	11	0	6	0	6	0	0	0	0	0
Benthic 65 mm (knot to knot)	–	0	0	0	0	0	0	0	0	0	0
Narva Reservoir											
Electrofishing	6	0	0.1	0	0	0	0	0.3	0	0.5	0
Benthic Nordic	–	10.3	0	6.3	0	0.7	6.3	0.7	0	0.3	0.3
Pelagic Nordic	–	0	0	20	0	1	0	0	7	0	0
Benthic 65 mm (knot to knot)	–	0	0	0	0	0	0	0	0	2	0
BPP channel											
Electrofishing	43	0	0.1	0	0	0	0	13	0.4	0	0
Benthic Nordic	–	10.3	0	11.3	0	10.7	0	0.3	0.3	0	1
Benthic 65 mm (knot to knot)	–	0	0	0	4	0	0	0	0	0	0

one individual belonged to the large group. The nitrogen isotopic values of Amur sleeper were between native fish and macroinvertebrate communities at all sampling sites, although large specimens were located at the same level with native fish species in the pond (Fig. 2).

SIBER model results indicated that Amur sleeper isotopic niches did not overlap with those of co-occurring native fish populations, except in Narva Reservoir, where it overlapped with tench (35%), spined loach (32%) and roach (14%). The isotopic niche (SEAc) of Amur sleeper was very wide in the pond (77.5‰^{2}) due to low carbon isotope values, while the niches were smaller in the channel and Reservoir (0.59‰^{2} and 0.88‰^{2}, respectively), compared to other fish species within each system. Only spined loach in the reservoir occupied a smaller niche area compared to Amur sleeper (Fig. 3, Table 2).

Stomach contents

The logistic regression curve indicated that Amur sleeper undergoes an ontogenetic shift from < 50% benthivorous to > 50% piscivorous diet at an individual total length (TL) of 8.7 cm (p = 0.004; 95% CI, Fig. 4).

Stomachs of all sampled Amur sleeper individuals (66) were analysed, of which 65 were 100% full, regardless of fish size and one was 90% full. The amount of the analysed stomachs of large and small individuals were respectively 4 and 13 from pond; 8 and 28 from Narva Reservoir and 1 and 12 from the channel. In all the invaded ecosystems, the Amur sleeper diet comprised mainly macroinvertebrates and, to some extent, fish. In the channel, only one individual represented the large group (TL > 8.7 cm), its stomach being 100% full of macrophytes and detritus. In all studied ecosystems, the diet of small (TL < 8.7 cm) specimens consisted mostly of macroinvertebrates (fragments), ranging from 17% in the channel to 46% in the pond, with Chironomidae, Trichoptera, Ephemeroptera and Odonata being the most common (Fig. 5). Larger (TL > 8.7 cm) Amur sleeper individuals had

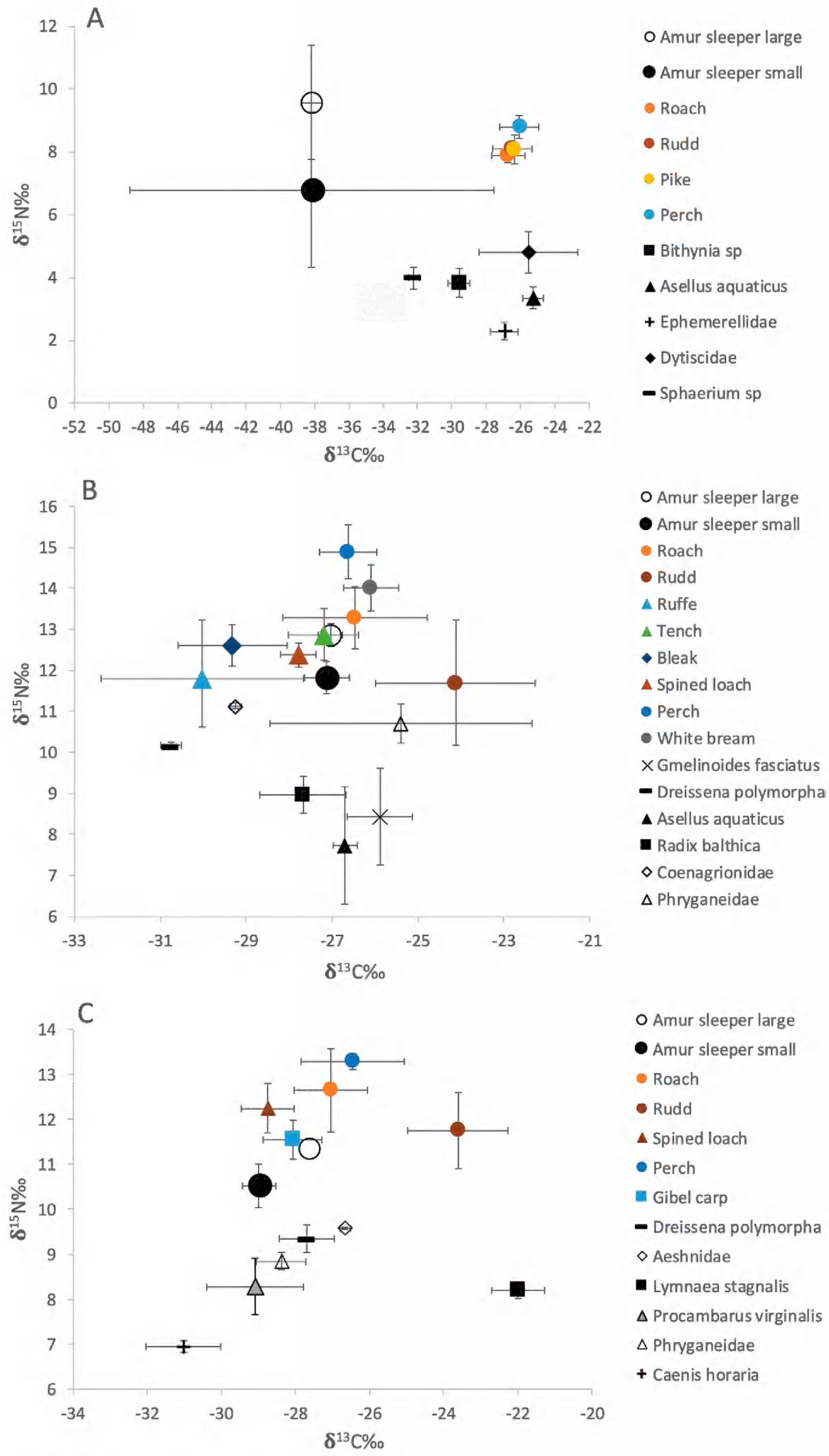

Figure 2. Carbon and nitrogen stable isotopes mean values (± standard deviation) of Amur sleeper large and small individuals (open and filled black circles), native fish species and macroinvertebrates, in the (**A**) pond, (**B**) Narva Reservoir and (**C**) BPP channel.

mainly fish in their diets, with the highest proportions in the reservoir (88%) and pond (50%) (Fig. 5). However, fish were also found in some smaller specimens, accounting for 4% of stomach contents in the reservoir and 17% in the channel. Zooplankton (14%) and Gammaridae (7%) were found only in stomachs of

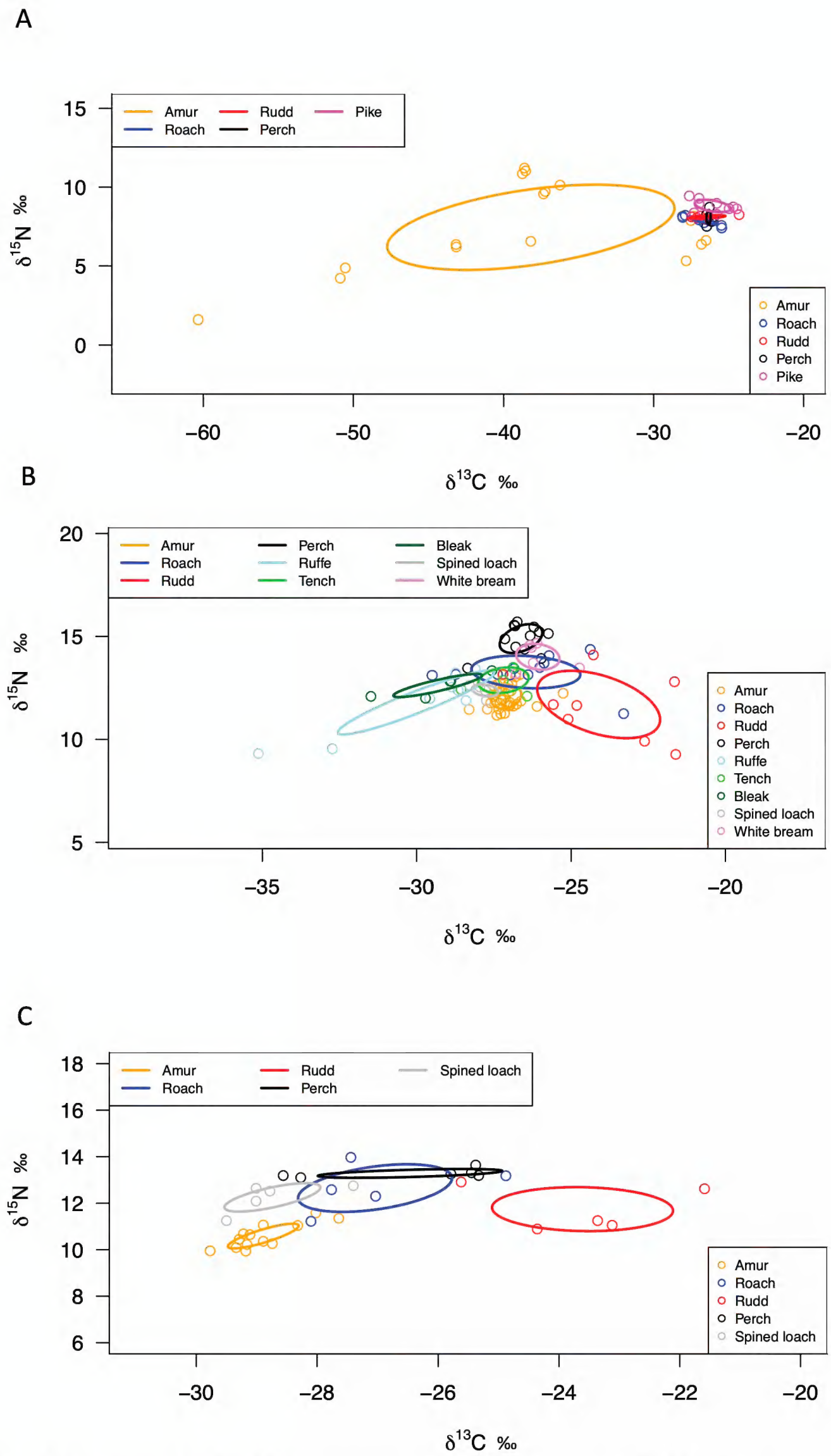

Figure 3. Isotopic niches of each fish species represented by ellipses and fish individuals represented by open circles in the (**A**) pond, (**B**) Narva Reservoir and (**C**) BPP channel.

smaller individuals in the reservoir. Although large prey items for Amur sleeper, gastropods and bivalves were also found in stomachs of both size-classes, with relatively high occurrence of gastropods in larger individuals in the pond and reservoir and with lesser occurrences of gastropods and bivalves in smaller specimens in the reservoir and channel (Fig. 5).

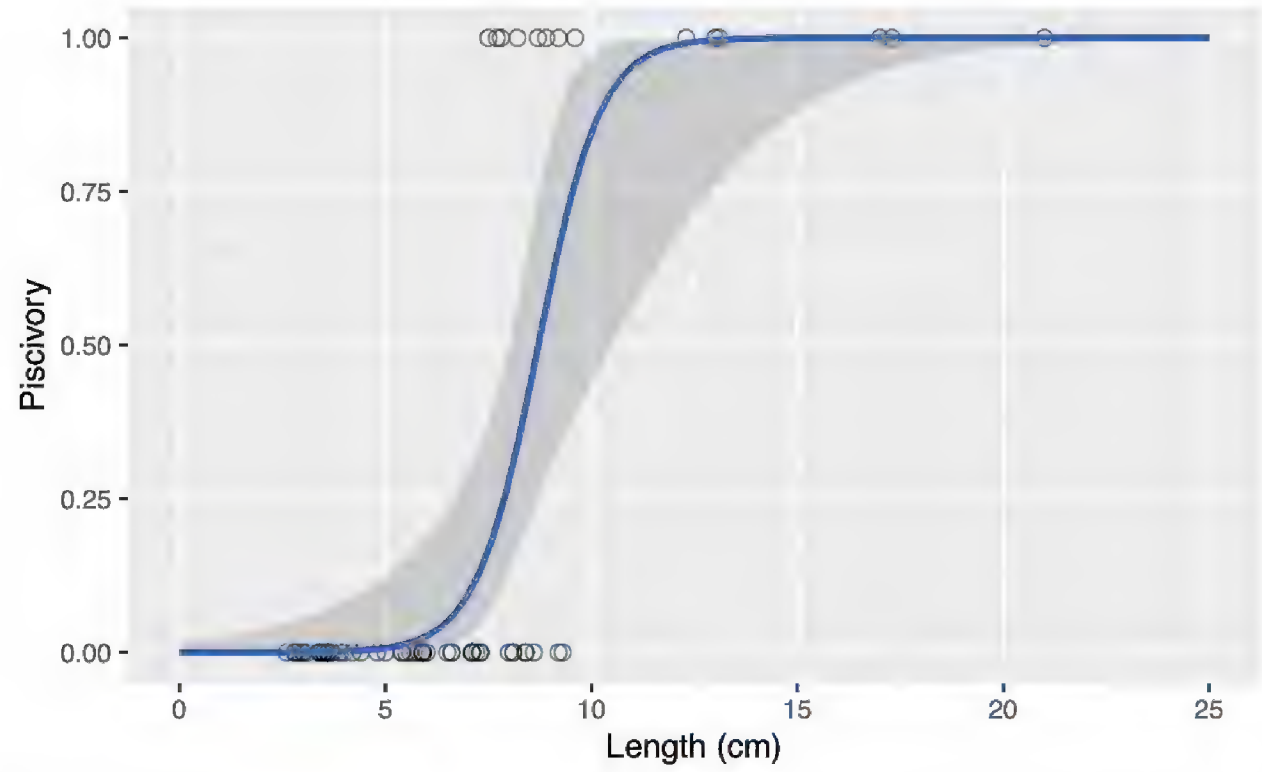

Figure 4. Logistic regression curve was fitted by the following equation $y = [e^{(-13{\cdot}226 + 0{\cdot}426x)}][1 + e^{(-13{\cdot}226 + 0{\cdot}426x)}]^{-1}$ showing ontogenetic diet shift from benthivory (0) to piscivory (1). Shadow area represents 95% Confidence Interval.

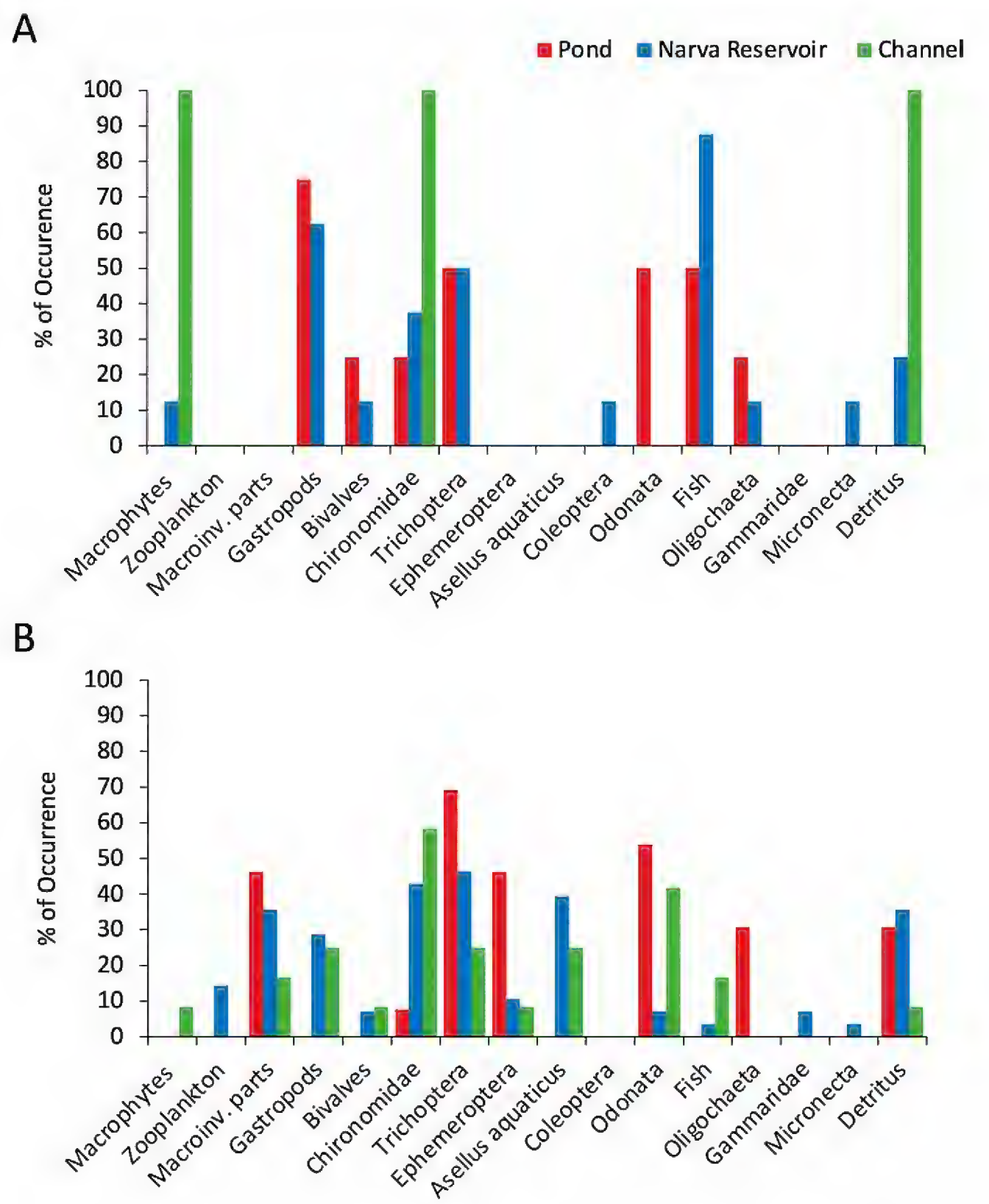

Figure 5. Prey items occurrence (%) in stomach contents of (**A**) large (total length > 8.7 cm) and (**B**) small (total length < 8.7 cm) Amur sleeper individuals in the pond, Narva Reservoir and BPP channel.

Discussion

Invasive Amur sleeper was well-established in each of the studied waterbodies and occupied the isotopic niche between predatory-omnivorous fish species and macroinvertebrates. In the reservoir and channel, the nitrogen isotope values of Amur sleeper, both large and small, show its intermediate role between bottom-up and top-down energy fluxes of the food web, while in the pond, large individuals had similar isotope values with native fish species. Yet, in the pond, the isotopic niche of Amur sleeper was much wider than those of co-occurring native fish. Substantial variations in nitrogen and carbon isotope values and much lower values for Amur sleeper compared to other fish, contributed to the wide isotopic niche in the pond. Low carbon SI values may indicate anoxic conditions at the pond bottom, favouring methanogenesis and conversion of methane to microbial biomass by methane-oxidising bacteria (MOB) (Jones and Grey 2011). MOB that have low carbon SI values can be consumed by invertebrate consumers, which transfer low SI value up to the top predators (fish) through trophic transfer (Ravinet et al. 2010; Sanseverino et al. 2012). Low carbon SI values and the wider isotopic niche of Amur sleeper in the pond may thus be the result of its occasional feeding on profundal macroinvertebrates that have consumed MOB (Eller et al. 2005; Jones and Grey 2011; Grey 2016). Exceptionally low carbon isotope values of small Amur sleeper individuals in pond indicate their higher assimilation of methane-derived carbon if compared to large individuals. Such feeding behaviour of small individuals widen the overall isotopic niche of Amur sleeper in the pond, with some individuals using energy sources mostly from profundal and some from littoral habitats.

Chironomidae and Oligochaeta feeding on MOB would be the best prey candidates for low carbon SI values. Unfortunately, we were not able to analyse SI values from these organisms, since the bottom of the pond was fully covered by macrophytes, preventing sampling of profundal benthic macroinvertebrates. However, amongst the sites and both size groups, highest proportions of Oligochaeta were found from stomachs of small Amur sleeper in the pond, suggesting that Oligochaeta was an important prey item and potential source for methane-derived carbon.

Invasive Amur sleeper is a predatory-omnivorous fish species mainly feeding on macroinvertebrates, but can be also piscivorous (Grabowska et al. 2009; Rau et al. 2017; Djikanovic et al. 2023). We hypothesised that its isotopic niche would consistently overlap with other fish species, particularly predatory-benthivores inhabiting littoral habitats, such as roach and perch. However, the isotopic niche of Amur sleeper only marginally overlapped with some native fish species (tench, spined loach and roach) in Narva Reservoir, but did not overlap with native fish in the pond or BPP channel. Results also indicated isotopic niche partitioning between Amur sleeper and co-occurring native fish populations. The ability of Amur sleeper to occupy an isotopic niche with limited overlap with ecologically similar native fish species may suggest an adaptation strategy, aimed at avoiding interspecific competition during its invasion and establishment in new ecosystems. Furthermore, we hypothesised that Amur sleeper has a wider isotopic niche than benthic native fish; however, our results showed the opposite. The Amur sleeper exhibited a narrower isotopic niche, indicating the use of different habitats and food sources compared to co-occurring native fish. These observations underscore the high level of adaptability and plasticity of Amur sleeper. However, the isotopic niche area of Amur sleeper could also depend on the diversity of native fish

community. A higher diversity of native fish community could imply higher interspecific competition, potentially leading to a reduced isotopic niche area of the invasive species. Conversely, lower diversity might allow for an expanded isotopic niche area for the invasive species (López-Rasgado et al. 2016). The relationship between niche width and community diversity is an intriguing aspect of Amur sleeper invasion and future isotope studies should focus on analysing more invaded ecosystems across a larger spatial scale.

In accordance with prior research (Koščo et al. 2008; Grabowska et al. 2009), our findings showed that Amur sleeper undergoes an ontogenetic dietary shift from benthivory to piscivory at a total length of 8.7 cm (± 95% CI), which is 1.7 cm longer than the shift size reported previously (Koščo et al. 2008; Kutsokon et al. 2021). The dietary differences between small and large specimens show a shift from smaller, more readily available prey to larger, more nutritious prey during the growth. This transition reflects changes in their ecological role, feeding capabilities and impact on the ecosystem. Our findings align with the results of previous studies (Koščo et al. 2008; Grabowska et al. 2009; Kati et al. 2015; Kutsokon et al. 2021), which observed that small Amur sleepers primarily consume high proportions of small and less motile macroinvertebrates, such as Chironomidae, Trichoptera, Ephemeroptera and Odonata. In contrast, larger Amur sleepers show a higher consumption of larger macroinvertebrates like gastropods and bivalves, as well as of more motile prey, such as Coleoptera and fish. In the pond and reservoir, where the Amur sleeper populations exhibited a greater occurrence of larger individuals, the proportions of fish prey found in their stomachs were higher compared to their smaller counterparts in the channel. A previous study conducted in the same pond found that Amur sleeper's diet consisted mainly of juveniles of its own and sunbleak (*Leucaspius delineatus*) (Tambets et al. 2010), showing high cannibalistic behaviour, as also reported in another study (Grabowska et al. 2009). Moreover, Tambets et al. (2010) found that the fish community in the studied pond was represented mostly by adult Amur sleeper, indicating strong predation on smaller individuals, not only by perch and pike, but also by larger conspecifics.

Pike were introduced in the pond to help control the Amur sleeper population. Similar to the findings of Rakauskas et al. (2019), pike specimens had a high growth rate and their food consisted exclusively of Amur sleeper individuals. This top predator could limit opportunities for Amur sleeper to prey on macroinvertebrates and forage in littoral habitats, thus increasing its reliance on piscivory and cannibalism. However, Amur sleeper individuals in our study had stomachs full of consumed food items, regardless of body size, highlighting its voracious feeding habits (e.g. Djikanovic et al. (2023)).

Amongst the prey items found in Amur sleeper stomachs, spined loach (*Cobitis taenia*) was identified. Spined loach is a protected fish species in Estonia (Kesler et al. 2009; Tammiksaar and Kangur 2020). The isotopic niches of Amur sleeper and spined loach overlapped substantially in the reservoir. This overlap, along with direct predation, suggests that the Amur sleeper may pose a significant threat to the endangered spined loach population in invaded habitats. These findings also suggest that Amur sleeper can threaten the protected weatherfish (*Misgurnus fossilis*), which has similar habitat preferences (Djikanović et al. 2023) and inhabits areas upstream of the Narva Reservoir, to where the Amur sleeper has not yet spread.

Interestingly, amongst species consumed by Amur sleeper, there were also different invasive species present, such as zebra mussels (*Dreissena polymorpha*),

amphipod (*Gmelinoides fasciatus*) and marbled crayfish (*Procambarus virginalis*), which are all well established in the studied waterbodies. All these invasive species occupy different trophic positions and could represent food sources for Amur sleeper, possibly facilitating Amur sleeper invasion and establishment. These results support the invasion meltdown hypothesis (Simberloff and Von Holle 1999), where the establishment of one invasive species can facilitate the establishment of others.

In our studied ecosystems, Amur sleeper can affect native communities at different trophic levels, especially native macroinvertebrate communities. These feeding characteristics exert both top-down and bottom-up effects, disrupting energy transfer to higher trophic levels. In a recent study, Kuparinen et al. (2023) quantified the potential effects of Amur sleeper on the food web of the not-yet-invaded, large Estonian Lake Võrtsjärv. Results showed that Amur sleeper invasion would decrease the biomass of native top predators, such as pikeperch, perch, pike and eel, which all have high fishery value, due to competition for benthic macroinvertebrate food and direct predation of the young native fish individuals. In contrast, the biomass of fish species inhabiting lower trophic levels, such as bream and smelt, was projected to increase, likely as consequence of reducing predation from the top predator.

Our findings showed that Amur sleeper may affect native fish communities in the studied ecosystems, serving as a warning for stakeholders and resource managers of the potential threats that this invasive fish species can pose on invaded and nearby, connected aquatic habitats.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

FE and MK- Conceptualisation. MT, EK and FE - Investigation. FE, MK, PT and AT- Formal analysis, data curation, methodology, software and visualisation. FE, MK, PT and TN - Writing original draft. FE, MK, PT, EK, MT, AT and TN - Writing, review and editing.

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Data availability

All of the data that support the findings of this study are available in the main text.

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